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Predicted range shifts of alien tree species in Europe

Radosław Puchałka^{a, b, *}, Sonia Paż-Dyderska^c, Andrzej M. Jagodziński^c, Jiří Sádlo^d,
 Michaela Vítková^d, Marcin Klisz^e, Serhii Koniakin^f, Yulia Prokopuk^{e, f}, Maksym Netsvetov^{f, g},
 Valeriu-Norocel Nicolescu^h, Tzvetan Zlatanovⁱ, Marcin Mionskowski^j, Marcin K. Dyderski^c

^a Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Poland

^b Centre for Climate Change Research, Nicolaus Copernicus University in Toruń, Poland

^c Institute of Dendrology, Polish Academy of Sciences, Kórnik, Parkowa 5, 62-035, Poland

^d Department of Invasion Ecology, Czech Academy of Sciences, Institute of Botany, CZ-252 43, Příhonice, Czech Republic

^e Dendrolab IBL, Department of Silviculture and Genetics, Forest Research Institute, Sękocin Stary, Poland

^f Department of Phytocology, Institute for Evolutionary Ecology, National Academy of Sciences of Ukraine, Kyiv, Ukraine

^g BIOGECO, University of Bordeaux, INRAE, Cestas, France

^h Faculty of Silviculture and Forest Engineering, Transilvania University of Brasov, Sirul Beethoven 1, 500123, Romania

ⁱ Institute of Biodiversity and Ecosystem Research, Bulgarian Academy of Sciences, Gagarin Street No. 2, 1113 Sofia, Bulgaria

^j Bureau for Forest Management and Geodesy, Leśników 21, 05-090 Sękocin Stary, Poland

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ABSTRACT

Alien tree species are considered both a threat to nature conservation and a base for forest management. We compiled species occurrences from biodiversity databases, forest inventories, and literature data. We modeled the availability of potential niches using the MaxEnt method and bioclimatic variables for current conditions, 2041–2060, and 2061–2080 periods. We used four climate scenarios: SSP126, SSP245, SSP370, and SSP485. The results confirm our hypotheses that, (i) coniferous species will contract, and deciduous trees will expand their climatic niche, (ii) a significant part of the areas where the studied species currently occur will be outside their climatic optimum in the coming decades; (iii) changes in the climatic optimum distribution will be greater in the 2041–2060 period than in 2061–2080. These predicted shifts are relevant for evidence-based management in sites already occupied by the studied alien trees. Our results are also relevant to the development of prevention and early detection measures in areas predicted to become climatically suitable for the studied species.

1. Introduction

European dendroflora comprises a significantly smaller number of species in comparison to North America and Asia, which is interpreted as a result of longitudinally distributed mountain ranges that hampered the migration of species during the Quaternary period (Bellon et al., 1977; Hermann, 1987; Svenning and Skov, 2007). In the last few centuries, the number of tree species in Europe has increased due to the intentional introduction of alien species (Bellon et al., 1977; Krivánek and Pyšek, 2008; Krumm and Vitkova, 2016; Nicolescu et al., 2020, 2018). Many exotic species demonstrate faster growth rates and are more resistant to water scarcity and biotic threats than native ones. Hence, in many European countries, they are cultivated on large-scale plantations (Brundu and Richardson, 2016; Hasenauer et al., 2016). About 150 alien tree species are currently cultivated or considered for planting in European forests (Brus et al., 2019; Dimitrova et al., 2022). However,

many of them are invasive and negatively affect biodiversity and the soil environment. Hence their deliberate propagation is restricted by legal regulations at the national level (Langmaier and Lapin, 2020; Pötzelsberger et al., 2020a). On the other hand, one of the greatest threats to European forests is climate change and the higher frequency of summer droughts, heat waves and late spring frosts (Liu et al., 2018; Puchałka et al., 2016; Sangüesa-Barreda et al., 2021). The negative effects of climate warming have been documented for species with the greatest ecological and economic importance in Europe, i.e. *Fagus sylvatica* L. (Martinez del Castillo et al., 2022), *Picea abies* (L.) H.Karst. (Bosela et al., 2021), and *Quercus robur* L. (Doležal et al., 2010). Therefore, assessing the potential forest tree habitat availability under a changing climate is urgent. For this purpose, a common tool is modeling the potential ecological niche using wide-scale maps containing the current and predicted future climatic conditions (Dyderski et al., 2018; Pecchi et al., 2019; Thuiller et al., 2005).

* Corresponding author at: Department of Ecology and Biogeography, Nicolaus Copernicus University in Toruń, Lwowska 1, PL-87-100, Toruń, Poland.
 E-mail address: puchalka@umk.pl (R. Puchałka).

Due to the anticipated climate changes, many major native European tree species will contract their potential niches (Bombi et al., 2017; Dyderski et al., 2018; Thurm et al., 2018) that consequently may be colonized by alien tree species. The latter are considered both a promising alternative to declining native trees and a serious threat to biodiversity (Pötzelsberger et al., 2020b; Thurm et al., 2018). Of particular concern is that recent research on the *Robinia pseudoacacia* invasive species in Europe suggests that we can expect most potential range changes to occur twenty years earlier than previously predicted (Puchałka et al., 2021). This can limit ability of trees migration decreasing probability of reaching reproductive age. This can also affect forest management, as trees can be unable to reach their economic rotation age (Zimová et al., 2020). Despite many arguments against introducing exotic species, they are considered for cultivation as species that ensure higher economic stability in forest management in the changing climatic conditions. Thurm et al. (2018) propose to maintain alien tree species under silvicultural control, thus introducing them rather in semi-natural managed forests than in natural forest communities. The most serious threats caused by the invasive alien species in natural forest ecosystems include species competition, soil changes and transmission of diseases (Langmaier and Lapin, 2020). Therefore, Global Guidelines for the use of Non-Native Trees (GG-NNTs, Recommendation 1; Brundu et al., 2020) recommend the use of native tree species over alien ones, and attention to the precise provenance of seeds and germplasm (Alizoti et al., 2022). If native tree species are not suitable, the consequent recommendation is to evaluate the use of aliens with low invasion risk. To mitigate the climate change effect, the assisted migration of the populations from areas with similar climatic conditions to those predicted in the future, as well as restoration of gene flow among populations, may support natural adaptation processes (Casazza et al., 2021). Essential for planning forest management strategy with economic benefits and avoiding the high costs associated with removing invasive species is to estimate the availability of areas suitable for the cultivation of particular tree species and areas where the spread of alien species may threaten biodiversity. Increasingly important for the management practices is consideration of the prioritization of alien species according to the magnitude of their environmental impacts using the standard protocol of EICAT - Environmental Impact Classification of Alien Taxa (Hawkins et al., 2015) or SEICAT - Socio-Economic Impact Classification of Alien Taxa (Bacher et al., 2018).

Woody angiosperm species established in Europe are members of phylogenetically distant families (Takhtajan, 2009). The most invasive tree species in Europe include mainly angiosperms such as *Acer negundo* L., *Ailanthus altissima* (Mill.) Swingle and *Prunus serotina* Ehrh. (Weber and Gut, 2004). In Central and Eastern European forests, also *Fraxinus pennsylvanica* Marshall and *Quercus rubra* L. are considered highly invasive species (Burda and Koniakin, 2019; Drescher and Prots, 2016; Dyderski et al., 2020; Prots et al., 2011; Riepsas and Straigytė, 2008). In contrast, gymnosperm species cultivated in Europe are mainly members of two families - Pinaceae and Cupressaceae (Brus et al., 2019; Farjon and Filer, 2013; Hasenauer et al., 2016). Although globally alien coniferous trees colonize a wide range of habitats, their invasiveness in Europe is poorly documented (Adamowski, 2004; Carrillo-Gavilan and Vila, 2010). In this group, *Pinus strobus* L. is considered to be the most widespread conifer species in Europe (Mandák et al., 2013; Münzbergová et al., 2013; Weber and Gut, 2004). *Pseudotsuga menziesii* (Mirbel) Franco has been naturalized in most European countries where this species was introduced (Carrillo-Gavilan and Vila, 2010). Naturalization of *Picea sitchensis* (Bong.) Carr. has been documented only along the Norway coast and in the British Isles (Nygaard and Øyen, 2017; Page and Cameron, 2006) and of *Pinus contorta* Douglas only in Scandinavia (Sykes, 2001). Spontaneous spread of other conifers, e.g., *Thuja plicata* Donn. ex D. Don has been observed rarely (Adamowski, 2004; Bellon et al., 1977), but this species has been also naturalized in Central Europe (Tokarska-Guzik et al., 2012). Dyderski et al. (2018), suggested

that conifers and early successional broadleaved species will mainly lose and late successional species will gain potential niches in a future warmer climate. It is worth noting that many tree species introduced to Europe, especially North American ones, come from places with a different distribution of annual precipitation. In Europe, most of the precipitation falls in the summer season and a small amount in the winter. In contrast, in North America, for example, the rainfall distribution is the opposite. As a result, alien tree species may be better adapted to summer droughts (Bellon et al., 1977; Huang et al., 2017; Song et al., 2021). This suggests that they may be better adopted the future European climatic condition with an expected higher frequency of summer droughts, than native trees.

So far, only some European alien tree species have predictions for their current and future ranges made for 2061–2080, e.g., *Quercus rubra*, *Pseudotsuga menziesii*, *Robinia pseudoacacia* (Dyderski et al., 2018). However, these studies were performed on occurrence data that poorly covered the distribution of these species in southeastern and eastern Europe and covered only the years 2060–2080. The poor representation of data from some regions was due to the unavailability of their biodiversity databases and the difficulty of supplementing them with data from other sources. A recent study of the distribution of *R. pseudoacacia* showed that the addition of occurrence data from regional databases of Eastern Europe and the literature gave a significantly different prediction result from that obtained in previous studies. Moreover, the magnitude of change in the potential range of this species, expected for 2061–2080, will already be observed in 2041–2060 (Puchałka et al., 2021). This, as well as the recent publication of new climate change scenarios (Riahi et al., 2017), creates the need not only to study potential range changes for species not previously studied, but also the need to update predictions for taxa previously studied, and to supplement forecasts for the 2041–2060 period. This is crucial because of the more urgent need than previously thought to develop strategies to mitigate the adverse effects of warming on forestry and conservation.

We aimed to determine changes in the distribution of climatically optimal areas for gymnosperm and angiosperm tree species considered as drought tolerant naturalized in Europe (Pötzelsberger et al., 2021; Wohlgenuth et al., 2022), with sufficient data coverage and reaching the southern limits of their ranges in Europe.

We hypothesize that (i) coniferous and the early successional deciduous species will lose, and the late successional deciduous species will expand their climatic niche, as native coniferous and the early successional deciduous species are more vulnerable to climate change (Dyderski et al., 2018); (ii) a significant part of the areas where the studied species currently occur will be outside their climatic optimum in the coming decades; (iii) changes in the distribution of optimal climatic conditions will be greater in years 2000–2050 than in 2050–2070 (Puchałka et al., 2021). In the face of the ongoing climate changes, the obtained results should be of significant practical importance for planning forest management and reducing the risk of biological invasions.

2. Materials and methods

2.1. Species studied and occurrence data

For testing our hypotheses we chose six conifers (*Abies grandis* (Douglas ex D. Don) Lindl., *P. sitchensis*, *P. contorta*, *P. strobus*, *P. menziesii*, and *T. plicata*, and six deciduous species (*A. negundo*, *A. altissima*, *F. pennsylvanica*, *Juglans nigra* L., *P. serotina*, and *Q. rubra*). The criteria for selecting alien species were (i) the possibility of collecting occurrence data from the entire European range of each species, (ii) the possibility of sampling the lower and upper ranges of thermal data sampling to capture the full or approximate tolerance range for thermal conditions, and (iii) the ecological and economic importance of the species in Europe (Brus et al., 2019; Hasenauer et al., 2016; Pötzelsberger et al., 2020b).

We compiled species distribution data based on internet databases: Global Biodiversity Information Facility (GBIF) (2012), Botanical Information and Ecology Network (BIEN) (Enquist et al., 2009), Pladias - Database of the Czech Flora and Vegetation, www.pladias.cz (Chytrý et al., 2021; Wild et al., 2019), iNaturalist (www.inaturalist.org), Plantarium (www.plantarium.ru), Flora Croatica (Nikolić, 2015), Vascular Plants of Hungary (Bartha et al., 2015), EU-Forest (Mauri et al., 2017), Biodiversity of Belarus (<http://florafauna.by>), Belarus Plant State Cadastre (<http://plantcadastre.by>), Polish State Forests IT System (SILP) (Starzycka, 2008), and Ukrainian Forest 'Ukrderzhisproekt' (<http://www.lisproekt.gov.ua/>). We filled the gaps in the occurrence data in Eastern Europe using Bulgarian and Romanian Forest Inventory

Data, literature references (Appendix A), and the authors' unpublished data.

The total number of collected occurrences for all study species was 465,534 and ranged from 3241 for *T. plicata* to 172,737 for *Q. rubra* (Table 1). Due to the different levels of mapping accuracy and different methods of site documentation (literature and herbarium materials with approximate location, sites documented with GPS receivers, centroids of forest divisions, and gridded occurrences from the distribution atlases), the distribution of species studied has been unevenly mapped (Fig. 1). The plant trait data (Table 1) comes from the Botanical Information and Ecology Network (BIEN) (Enquist et al., 2009) and the Plant Trait Database (TRY) (Kattge et al., 2020) databases.

Table 1
Studied species, their life-history traits, number of data points, and model characteristics.

Species	Max height [m]	Specific leaf area [cm ² g ⁻¹]	Wood density [t m ⁻³]	Number of input points	Number of points after resampling	AUC	probability occurrence threshold
<i>Abies grandis</i>	78.3	99.0	0.350	4346	1182	0.965	0.228
<i>Acer negundo</i>	33.5	252.1	0.454	26,959	4075	0.895	0.431
<i>Ailanthus altissima</i>	33.2	310.7	0.522	28,172	2730	0.950	0.405
<i>Fraxinus pennsylvanica</i>	43.9	211.6	0.530	4398	900	0.920	0.227
<i>Juglans nigra</i>	45.0	187.4	0.510	3420	1563	0.931	0.182
<i>Picea sitchensis</i>	78.6	55.6	0.365	50,127	1827	0.973	0.271
<i>Pinus contorta</i>	50.0	33.1	0.407	10,281	1247	0.979	0.196
<i>Pinus strobus</i>	45.7	110.7	0.350	19,278	2230	0.956	0.286
<i>Prunus serotina</i>	44.2	195.2	0.465	81,896	2159	0.956	0.296
<i>Pseudotsuga menziesii</i>	91.4	80.9	0.470	65,025	3608	0.944	0.334
<i>Quercus rubra</i>	75.0	157.9	0.453	172,737	4444	0.926	0.419
<i>Thuja plicata</i>	78.0	74.0	0.310	3241	878	0.957	0.459

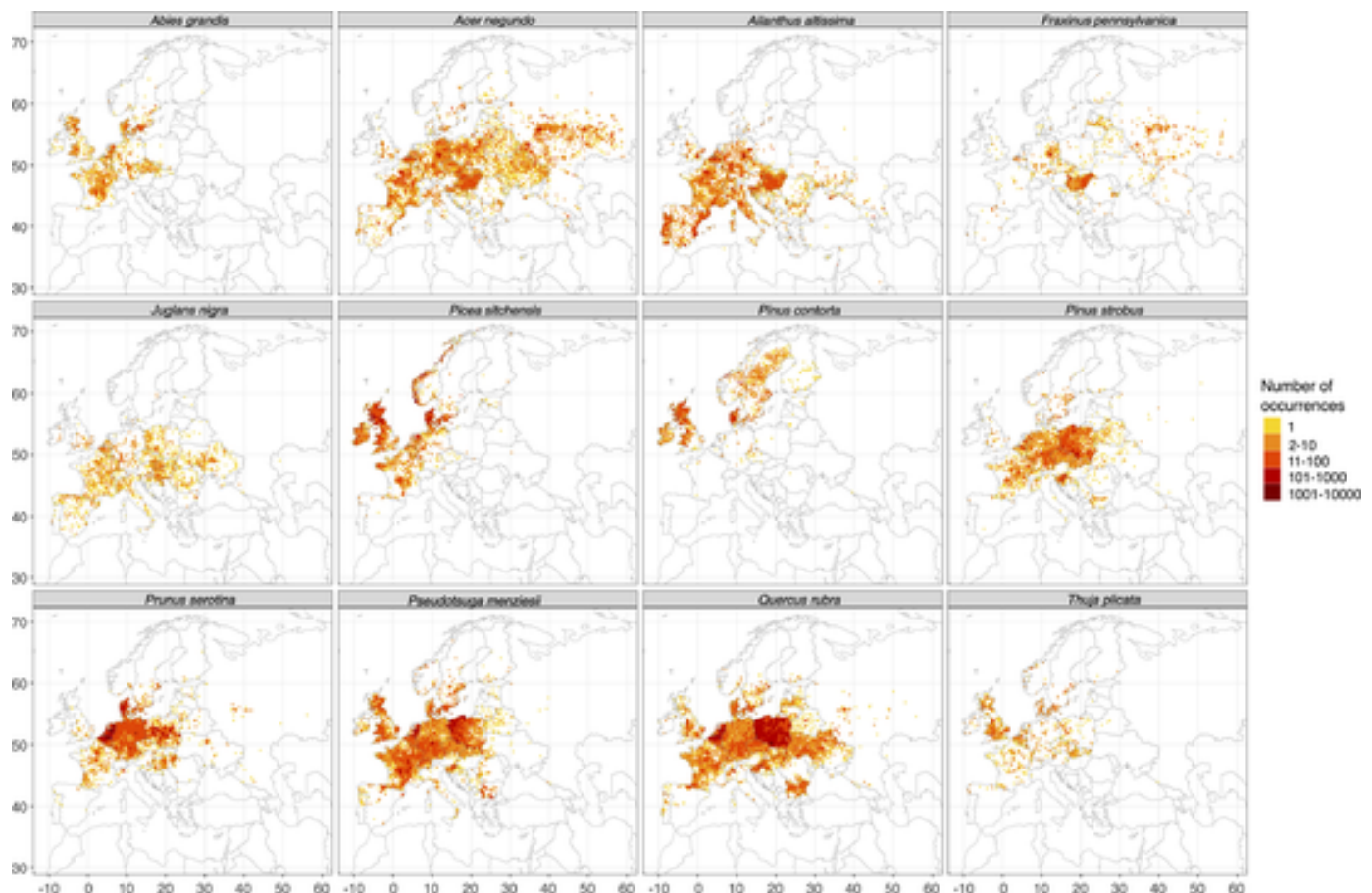


Fig. 1. Distribution of studied alien tree species in Europe according to the biodiversity databases supplement by the literature and forest inventory data.

In this study, we only used data from the invasive range of the species in our species distribution models, and did not include data from the native range. This is because including data from the natural range of an invasive species can introduce more bias than not including them. Many studies in forestry, evolutionary biology and biogeography have shown that species exhibit greater variability within their natural ranges than in the areas of introduction or invasion (Dar et al., 2020; Hintsteiner et al., 2018; Neophytou et al., 2020; van Loo et al., 2019). This is because only part of the gene pool is transferred to new areas during migration, and the genetic variability of natural populations is spatially distributed and subject to long-term environmental selection pressures. Local populations exhibit varying degrees of tolerance to environmental conditions, including climate. This is a well-documented phenomenon, and in the case of trees, it is also the subject of practical research in provenance trials (Guo et al., 2022; Klisz et al., 2019b, 2019a). Furthermore, the artificial range does not contain all variability of the species, and migration is limited by the physical barrier of oceans. Therefore, incorporating variability which is not present in the area of introduction into the analysis seems highly unreasonable. It is more logical to adopt an approach that considers only the ecological variability/climate tolerance present in the area of introduction. Moreover, the genetic foundations of that claim had been proven in studies using SDMs based on both native and invasive ranges. In the case of species differing in climatic niches between alien and native ranges, using predictions from each of them lead to various conclusions (Langdon et al., 2019). We agree that adopting such an approach may result in underestimating the potential ranges, given that alien species have not yet occupied all potential distribution areas. However, it should be noted that even numerous species native to Europe have yet to occupy their full potential range, despite some ten thousand years having passed since the retreat of the ice sheet (Svenning and Skov, 2004). Therefore, numerous studies on alien tree species distributions in Europe revealed the patterns evidenced by studies on biogeography and invasion ecology using that approach, e.g., not to introduce variation that is absent in Europe (Dyderski et al., 2018; Puchałka et al., 2021).

2.2. Climatic data

We used future climate projections provided by the IPCC 6th Assessment Report, based on Shared Socioeconomic Pathways (SSPs) (Riahi et al., 2017). These scenarios reflect uncertainties in possible trajectories of climate change mitigation. We chose four scenarios available in the WorldClim 2.1 database: SSP126 (sustainability, the most optimistic scenario reflecting RCP2.6 from the 5th report), SSP245 (a middle of the road, moderate scenario reflecting RCP4.5), SSP370 (regional rivalry, not used in the 5th report) and SSP485 (fossil-fuel based development, reflecting RCP8.5). For each SSP we used outcomes of four global circulation models (GCMs): IPSL-CM6A-LR (France), MRI-ESM2-0 (Japan), CanESM5 (Canada), and BCC-CSM2-MR (China), representing half of eight available GCMs for all four SSPs. We downloaded a dataset of 19 bioclimatic variables in a 2.5' resolution, derived from monthly temperature and precipitation records, and widely used for modeling species distributions (Booth, 2018; Booth et al., 2014; O'Donnell and Ignizio, 2012). To reduce multicollinearity, we calculated the Pearson correlation coefficient between bioclimatic variables. Then we removed the autocorrelated variables. We assumed $|r| > 0.7$ as a collinearity threshold. The final set of variables used for model development included seven bioclimatic variables (Table S2).

2.3. Data analysis

2.3.1. Potential niche modeling

To reduce over-sampling in some regions and under-sampling in others (Fig. 1), we randomly chose only one occurrence from each 0.25° grid raster cell for MaxEnt analysis, following an approach used in pre-

vious studies (Anibaba et al., 2022; Dyderski et al., 2018; Puchałka et al., 2023, 2021; Rocchini and Garzon-Lopez, 2017). This resulted in a more even representation of particular regions and prevented overrepresentation of the most intensively sampled regions. This way, we included 25,661 sites in the set of occurrences used for modeling. The highest number of occurrences that we used was 4444 sites for *Q. rubra*, and the lowest 878 sites for *T. plicata* (Table 1). Yet, this number is sufficient for MaxEnt analyzes (van Proosdij et al., 2016). Then, we divided datasets into a training set (80% of observations), used for model development, and an independent validation set (20% of observations). Due to presence-only distributional data, we used the MaxEnt algorithm to develop species distribution models. MaxEnt has been developed to process presence-only data (Elith et al., 2011; Phillips et al., 2006). In contrast to parametric models and other classification tools, MaxEnt does not need absence data in the theoretical assumptions, but instead it uses background data (so-called pseudoabsences). We used default MaxEnt settings. For each species, we randomly selected 10,000 pseudoabsence points (background points). Although using default number of pseudoabsences unbalance the input dataset, it reflects the frequency of particular studied species. We therefore decided to maintain consistency with previous studies, based on default number of pseudoabsences. As we calculated a threshold based on the highest sum of specificity and sensitivity, our results balance the high level of negative observations, which is typical of species that already did not fulfill all climatically suitable sites. The prevalence of background points makes the model more conservative, as it requires a stronger signal than it would in the case of equal proportions of presences and pseudoabsences (Elith et al., 2011).

We assessed the model quality using the area under receiver operator curve (AUC), as a metric depending on true positive and true negative rates (i.e., rates of positive and negative overlapping of the real and predicted occurrence). The output of the MaxEnt model is the probability that particular species can occur in a particular raster cell. To obtain presence-absence information, we calculated the threshold – the probability value with the highest sum of the sensitivity (true positive rate) and specificity (true negative rate). Such an approach balances false negatives and false positives (Fielding and Bell, 1997). The MaxEnt model also provides information about variable importance, expressed as percentage contribution to the model. We used the *dismo* package (Hijmans et al., 2020) for the development of the MaxEnt models development and the *raster* (Hijmans, 2020) and *sf* (Pebesma, 2018) packages for spatial data processing. We calculated potential range saturation as a proportion of sampled points and the number of pixels suitable for a particular species occurrence according to the model.

2.3.2. Predicted changes in species distributions

We applied the models to maps of current and future climatic scenarios to obtain predictions of species distributions. For each SSP, we averaged predicted species occurrence probabilities across the four GCMs (Appendix B, Fig. S1-S24). Similarly to previous research (e.g., Goberville et al., 2015; Paż-Dyderska et al., 2021; Thuiller et al., 2019), we presented the uncertainty of each prediction as maps of the standard deviation (SD) among GCMs (Appendix B, Fig. S25). Then, maps with threshold values (true/false) were used to estimate the changes in potential range, changing the values on maps with the future potential range from 1 to 2 (Puchałka et al., 2021). As a result of the calculations presented below, four different variants of changes in the range of the species were estimated: (i) areas still unsuitable for colonization ($0-2 \times 0 = 0$) – no changes, the species was not present, and the conditions will remain unsuitable for colonization, (ii) range expansion ($0-2 \times 1 = -2$) – areas potentially suitable for colonization, (iii) range contraction ($1-2 \times 0 = 1$) – areas where the species is currently present, but will fall outside the future optimum climate, (iv) persistence ($1-2 \times 1 = -1$) – areas where the species is currently present and will remain within the optimum climate (Puchałka et al., 2021).

3. Results

3.1. Quality of potential distribution models

The quality of the models as measured by AUC values ranged from 0.90 to 0.98 (mean = 0.95 ± 0.02) (Table 1). The potential distribution models for each species differed in contributions of the bioclimatic variables (Table 2). For coniferous species, the most important variable was Temperature Annual Range (bio7), except for *P. strobus* where Mean Temperature of Coldest Quarter (bio11) and Precipitation of Warmest Quarter (bio18) had higher importance. For four out of six broadleaved species studied Precipitation of Warmest Quarter was the most important predictor, while for two (*A. altissima* and *J. nigra*) it was the second most important predictor, after Mean Temperature of Coldest Quarter.

3.2. Predicted changes in species distributions

We found slight northward and eastward range shifts of coniferous species studied in all analyzed scenarios and timelines, with the highest eastward gains for *P. strobus* and *P. menziesii* (Fig. 2). All coniferous species studied will contract their range in Central Europe except for *P. strobus* and *P. menziesii*, and in continental Western Europe. Potential range of *A. grandis*, *P. contorta*, *P. sitchensis*, and *T. plicata* will be limited to the British Isles, coastal Scandinavia, Denmark, Netherlands and NW Germany. For *P. menziesii*, we also predicted occurrences in Western Germany, Northern France, Finland, Sweden, and mountain ranges. We predicted the lowest loss of climatic optimum for *P. strobus*, which would persist in most of its currently optimal areas.

We found that all broadleaved tree species studied are predicted to expand their range northeastwards, with the highest gains for *A. negundo* and *F. pennsylvanica* (Fig. 3). We predicted the highest northward shifts for *P. serotina* and *Q. rubra*. Almost all studied broadleaved species (except for *A. altissima*) will lose their southeastern range, especially *Q. rubra*, *A. negundo*, and *F. pennsylvanica*. For *Q. rubra* and *P. serotina* we also expect losses of the southern and southwestern parts of the current climatic range. In the case of both broadleaved and coniferous species, the majority of changes predicted for 2061–2080 will already occur by 2041–2060.

3.3. Range expansion and contraction

Climatic niche breadth for all broadleaved species and *P. strobus* under all examined climate change scenarios will be wider than for current conditions (Fig. 4). We predicted the highest range expansion for *P. serotina* and *A. altissima*, while the lowest – for *P. contorta*, *P. sitchensis*,

Table 2

Importance of bioclimatic variables (%) for particular species. The most important variable for each species was bolded: bio2 - mean diurnal range (mean of monthly (max temp - min temp)), bio7 - temperature annual range, bio8 - mean temperature of wettest quarter, bio11 - mean temperature of coldest quarter, bio15 - precipitation seasonality (coefficient of variation), bio16 - precipitation of wettest quarter, bio18 - precipitation of warmest quarter.

Species	bio2	bio7	bio8	bio11	bio15	bio16	bio18
<i>Abies grandis</i>	0.65	49.65	1.54	17.41	3.47	0.88	26.40
<i>Picea sitchensis</i>	1.65	74.99	0.50	3.36	0.50	0.28	18.73
<i>Pinus contorta</i>	3.56	35.61	20.08	5.85	2.15	1.36	31.38
<i>Pinus strobus</i>	1.56	23.31	2.76	30.45	0.07	0.79	41.05
<i>Pseudotsuga menziesii</i>	0.85	42.29	1.09	21.83	0.36	0.57	33.00
<i>Thuja plicata</i>	2.87	42.10	0.75	24.68	1.21	0.84	27.54
<i>Acer negundo</i>	4.40	2.04	11.93	23.87	1.43	2.68	53.64
<i>Ailanthus altissima</i>	3.22	6.94	2.87	55.71	1.24	7.02	23.01
<i>Fraxinus pennsylvanica</i>	0.96	0.82	37.25	16.96	3.58	0.77	39.66
<i>Juglans nigra</i>	5.89	11.23	4.85	39.48	1.09	1.25	36.21
<i>Prunus serotina</i>	2.08	15.98	1.37	37.09	0.73	3.10	39.65
<i>Quercus rubra</i>	1.70	4.35	2.36	39.59	0.08	1.60	50.32

and *T. plicata*. Simultaneously, we predicted the highest range contraction for these three species. We also found the highest magnitudes of range shifts in SSP485, and the lowest in SSP126 scenarios. For all species studied at least half of predicted climatic optimum shifts for 2061–2080 will occur by 2041–2060. Especially, for coniferous species studied these will be ca. 75% of predicted changes.

4. Discussion

Our study provided the potential distribution models of twelve alien tree species that are considered the most important ecologically and economically in the temperate zone of Europe (Brus et al., 2019; Hasenauer et al., 2016; Pötzelsberger et al., 2020b). For all species studied, except for *P. menziesii* and *Q. rubra*, this is the first study of this kind performed on the whole European range of their introduction. For those two species, we updated the previous study using occurrences significantly supplemented in comparison to the previous research (Dyderski et al., 2018) on sites from eastern and southeastern Europe. Similarly to our previous research on *R. pseudoacacia* (Puchałka et al., 2021), complete sampling from the entire study area gave the yielded results indicating greater risk of losing niches in southern Europe and that the ranges would shift north and northeast further than it was found in previous studies (Dyderski et al., 2018). Moreover, we analyzed two periods, 2041–2060 and 2061–2080, while the former has been often omitted in previous studies. The results for all twelve species confirmed our expectations that most of the forecasted changes in potential ranges for 2061–2080 can be observed over twenty years earlier (Figs. 2 and 3), as suggested by our earlier study on *R. pseudoacacia* (Puchałka et al., 2021). We demonstrate that most of the studied conifers will contract their potential ranges with climate change, while deciduous trees, also early successional species will mainly gain new areas for colonization (Figs. 2–4).

4.1. Study limitations

The AUC values for models > 0.90 indicated a very good performance of models (Elith et al., 2011). However, we are conscious that AUC-based assessment of model quality depends on species abundance and niche breadth (Dyderski et al., 2018), as well as on species traits and human activity related to introductions (Hanspach et al., 2010). Regarding future predicted ranges, as our models do not take into account migration rate, our conclusions refer to the 2nd ('Change in the climatically suitable area') and 5th ('Change in average climatic suitability in already occupied cells') measures of risks (Ohlemüller et al., 2006). We overcame the disadvantage of the high variability among GCMs (Goberville et al., 2015; Paż-Dyderska et al., 2021; Thuiller et al., 2019) by averaging predictions over GCMs and providing uncertainty estimations for each species and scenario. Another issue affecting our inference is the lack of niche saturation, connected with the relatively short time since the introduction of the studied species (Kowarik, 1995). In past some of studied species experienced shorter (e.g., *P. serotina*) or longer (e.g., *Acer negundo*) lag phase, which shaped their propagule pressure and dispersal capacity in past. On the one hand, climate change can shorten the lag phase between establishment and exponential growth of populations, as it can create more favorable climatic conditions for reproduction. On the other hand, it can also prolong the lag phase if a generation has already adapted to the previous climatic conditions. Therefore, not all potentially suitable sites have been already colonized, decreasing the breadth of the predicted climatic niche, which might be either the effect of climate change or past dispersal limitation, due to elongated lag phase. Moreover, bioclimatic models are unable to account for microhabitat variability and interspecies interactions that may affect habitat suitability (Dyderski and Pawlik, 2020; Thurm et al., 2018). Our conclusions are also limited by lack of fulfilling one of a key assumptions of species distribution model-

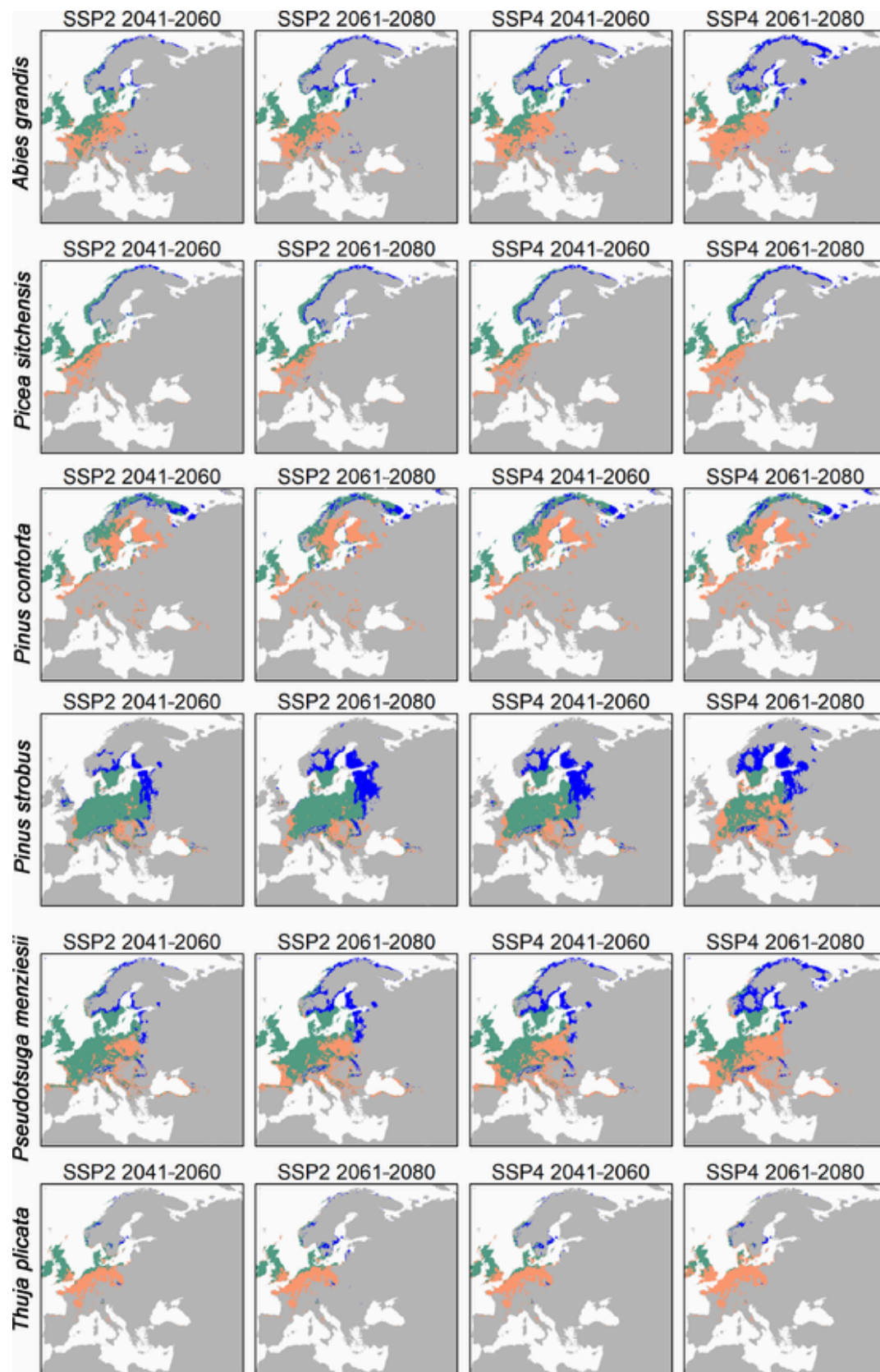


Fig. 2. Current and projected ranges of six studied coniferous tree species. Explanations: green + orange – current potential distribution, green – persistence, orange – future range contraction, blue – future range expansion, gray – still unsuitable.

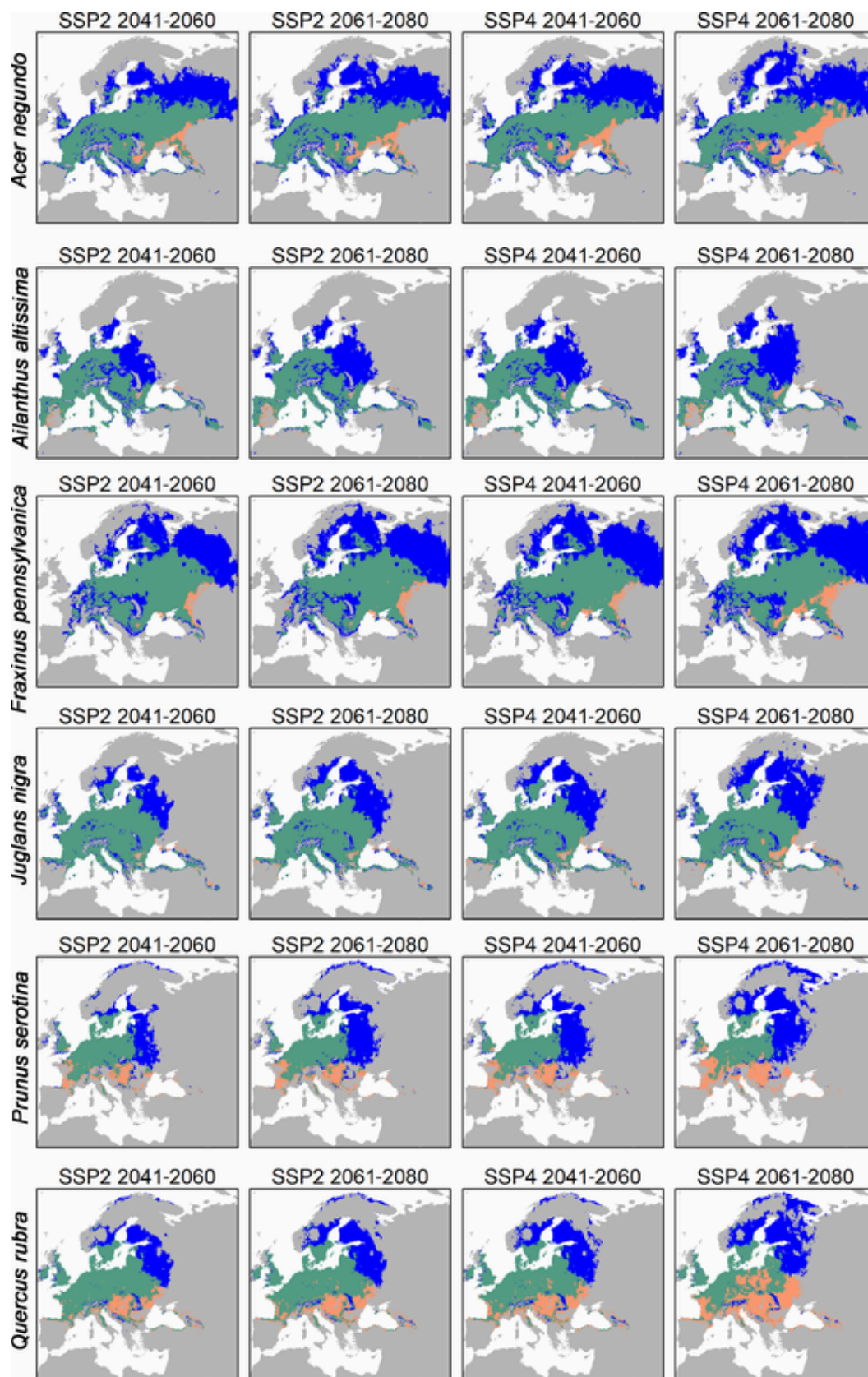


Fig. 3. Current and projected ranges of six studied deciduous tree species. Explanations: green + orange – current potential distribution, green – persistence, orange – future range contraction, blue – future range expansion, gray – still unsuitable.

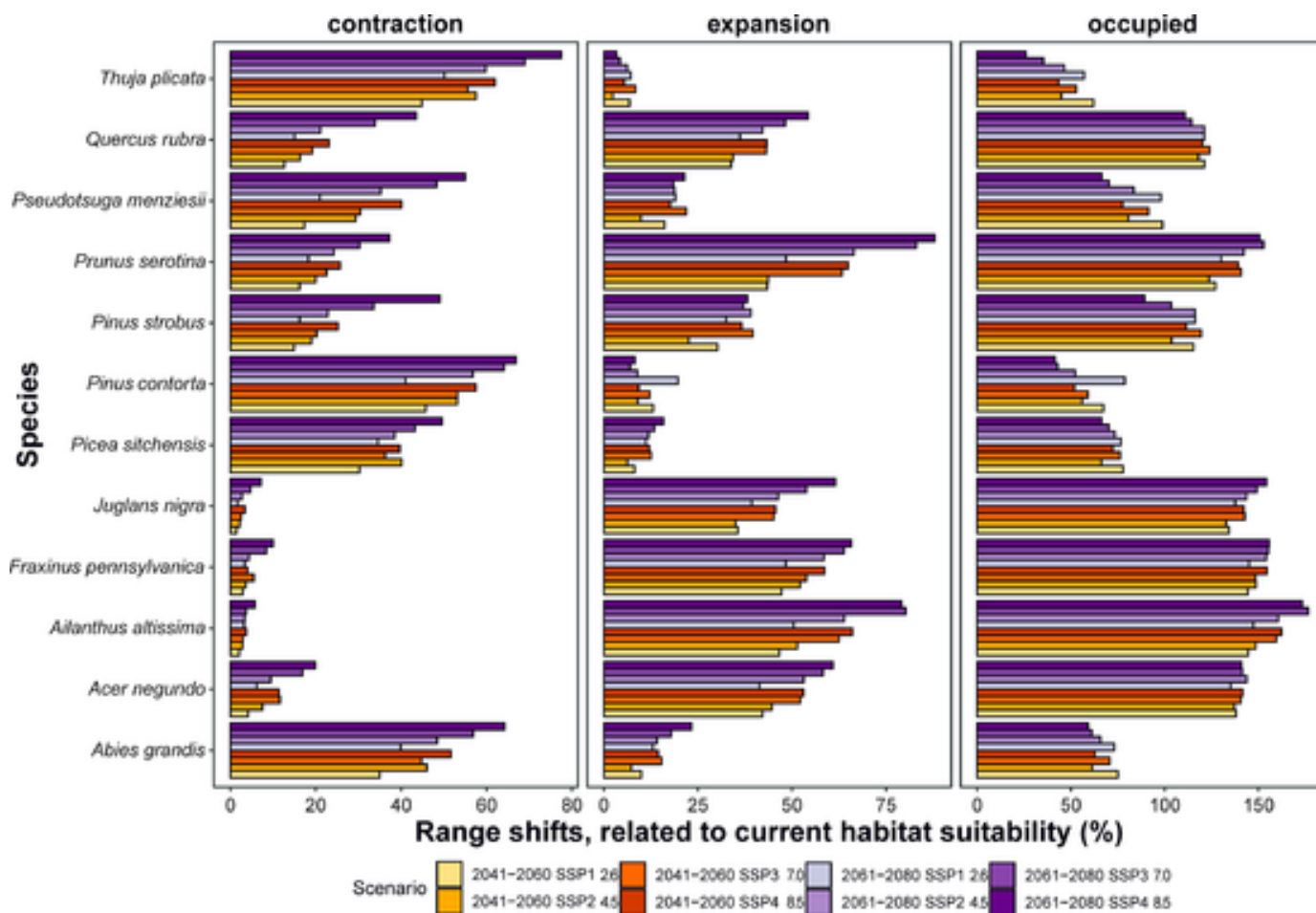


Fig. 4. Range shifts of studied alien tree species in four scenarios and two timelines of the climate change.

ing, that is equilibrium in niche dynamics (Hui, 2022). However, in Europe, and other areas where post-glacial recolonization did not finish, even native species fulfill on average 38.3% of potential niche (Svenning and Skov, 2004). Therefore, under such circumstances, modeling species distribution is quite often biased by that issue. Inferences about range expansion must take this uncertainty into account.

Some studies have shown that water shortages caused by river regulation had more substantial impact on the condition and growth of trees than climate change (Koprowski et al., 2018; Netsvetov et al., 2021, 2019). Trees survival also depend on soil properties, especially granulation, determining soil water-holding capacity (Polláková et al., 2021) and the topographic shape of the terrain, which strongly differentiates the local thermal and humidity conditions (Lembrechts et al., 2022; Sewerniak and Puchałka, 2020). Hence, some sites may create microrefugia with an optimal microclimate for declining species (Dyderski and Pawlik, 2020; Lenoir et al., 2017). Tree survival may also depend on various sensitivity of trees to extreme meteorological conditions depending on the age and size of individuals (Bellon et al., 1977; Sanchez-Salguero et al., 2018), and on vulnerability to herbivores and pathogens (Forrest, 2016; Jactel et al., 2019; Seidl et al., 2018).

4.2. Differences between predictions for 2041–2060 and 2061–2080

According to our expectations, the analyzes performed using current (Riahi et al., 2017) climate change scenarios, similar to Puchałka et al. (2021), show that we can expect the most significant changes in the potential ranges of species by 2041–2060. However, the availability of climatic niches in 2041–2060 and 2061–2080 should be relatively stable compared to the previous period. Generally, most of the studied

conifers will lose optimal areas for their colonization and cultivation, and oppositely angiosperms will mainly gain them (Figs. 2–4). Overall, for all species tested, potential ranges are expected to shift northeast, while in North America, gymnosperm ranges are forecasted to move northward and angiosperms more westward (Fei et al., 2017). However, the question of how well the gymnosperms will cope with the novel climate has not been answered yet (Klisz et al., 2022). In many areas, especially in the southern margin of species distributions, climatic optima do not persist between the studied periods longer than about twenty years. This suggests that, especially when cultivating species with a long production cycle, such as *Q. rubra*, there may be a high risk of not reaching rotation age in many areas, where they are considered as drought and heat resistant alternatives to native conifers and oaks (Chakraborty et al., 2019; Thurm et al., 2018). Persistence of these species will be stable in predicted areas up to 2070s. It appears that the disappearance of the studied species will depend on their ability to acclimatize to the rapid changes in climate and local habitat conditions.

4.3. What will be the consequences of changes in the studied species potential ranges for nature conservation and forest management?

Gymnosperms are generally considered less invasive in Europe than angiosperms. This is explained as an effect of competition from phylogenetically and ecologically similar native species, their reproductive traits and a long lag phase (Carrillo-Gavilan and Vila, 2010; Richardson and Rejmánek, 2004). Other researchers suggest that it is also related to too large or too small disturbances in ecosystems, limiting the areas suitable for colonization of European ecosystems (Adamowski, 2004). Here we covered the most invasive coniferous tree species – *P. menziesii*,

P. contorta, *P. sitchensis* and *P. strobus* whose naturalization in Europe has been sufficiently documented (Fanal et al., 2021; Nuñez et al., 2017; Nygaard and Øyen, 2017; Sykes, 2001). However, our results indicated that the further spread of all of them would be limited in the future by climate change (Figs. 2 and 4). The exception is *P. strobus*, considered to be the most widespread alien conifer species in Europe (Hadincová et al., 2007; Mandák et al., 2013; Weber and Gut, 2004) suppressing native vegetation by forming dense monocultural stands with a thick layer of needle litter (Hadincová et al., 2007), and outcompeting the native *P. sylvestris* by crown competition (Máková, 2008). Under all considered climate change scenarios *P. strobus* will be the only coniferous species with higher range expansion than contraction (Fig. 4). Nevertheless, this species has high sensitivity to some climate events, especially a synergism between the lack of precipitation and high temperature during the vegetation period (Klisz et al., 2022; Vacek et al., 2021). The spread of this species will be further limited by the high mortality caused by insects and fungal pathogens (Radu, 2008; Vacek et al., 2021). Observations from both native and secondary ranges show that *P. strobus* competes best on well drained sandy soils of low to medium site quality and invasion risk is the highest on these habitats (Máková, 2008; Mandák et al., 2013; Wendel and Smith, 1990). On the other hand, it can be very productive but usually occurs only as individual trees or in small groups on poorly drained soils (Upřety et al., 2014).

The second most widespread naturalized conifer species, *P. menziesii* (Carrillo-Gavilán et al., 2012; Carrillo-Gavilán and Vila, 2010; Nicolescu et al., 2023), according to this and our previous study (Dyderski et al., 2018), is expected to lose the majority of its potential climatic suitability. From the nature conservation point of view, this probably means that this species will become less invasive. On the other hand, from the viewpoint of forest management, it means significant economic losses, because in many areas it is planted as an alternative to native conifers that is more resistant to summer droughts and climate warming (Hoffmann et al., 2018; Lévesque et al., 2014). Northeastern Europe, where this species is expected to shift its niche, has a harsh continental climate with extreme weather conditions such as late spring frosts (Menzel et al., 2015; Puchałka et al., 2017, 2016). According to recent studies, warming in winter will negatively impact *P. menziesii* on the early germination rate, but does not affect late germinated seeds (Jastrzębowski et al., 2021). However, populations of plants with later phenology are usually less exposed to extreme weather conditions before spring, determining their higher survival rate (Guo et al., 2022; Silvestro et al., 2019). Other studied conifers (*P. sitchensis*, *P. contorta*, *T. plicata* and *Abies grandis*) spread only locally in northern Europe (Bellon et al., 1977; Fanal et al., 2021; Nygaard and Øyen, 2017; Sykes, 2001), and are evolutionarily adapted to cooler and milder climate (Farjon and Filer, 2013) and will lose a significant part of their climate niches in Europe. These species already occur in most of the northernmost land areas of Europe, and their ability to shift further northward and to higher altitudes is limited (Fig. 2). The cultivation of the coniferous tree species may also be associated with a high risk of co-invasions and biotic hazards, as they frequently exhibit significant damage caused by the native and introduced pests (Nuñez and Dickie, 2014; Pietras et al., 2018; Pötzelsberger et al., 2021).

In contrast, almost all studied angiosperms (except *J. nigra*) are actually among the most widespread tree species in Europe (Fig. 1) (Drescher and Prots, 2016; Weber and Gut, 2004). Generally, we predicted that these species would lose a small proportion of climatically suitable range at the southern edges. However, we did not predict loss of climatic suitability in most of their currently suitable ranges in the future. We also predicted that these species would gain climatically suitable areas in northern and northeastern Europe (Fig. 3). This group includes light-demanding early successional species such as *A. altissima*, *F. pennsylvanica* and *A. negundo*, which spread mainly in open, semi-open and disturbed areas, such as ruderal areas, river valleys, aban-

doned fields and forest gaps (Paž-Dyderska et al., 2020; Saccone et al., 2013; Straigytė et al., 2015). *A. altissima* is a thermophilous species (Kowarik and Säumel, 2007; Pyšek et al., 2002). Also, *F. pennsylvanica* growth is positively correlated with temperature, while *A. negundo* tree-rings do not show clear relationships with temperature (Zajdler et al., 2019). On the other hand, shade-tolerant late successional species e.g. *J. nigra*, *Q. rubra*, and *P. serotina*, spread mainly in forest communities (Pyšek et al., 2012). Thus, all studied angiosperm trees have many habitats optimal for colonization in Europe. Similarly to *R. pseudoacacia*, they will retain most of the current potential distribution and gain large areas optimal for colonization in eastern-northeastern Europe and more elevated sites (Fig. 3) (Dyderski et al., 2018; Puchałka et al., 2021). Only two species potentially valuable for forest management (*J. nigra* and *Q. rubra*) may lose climatic optimum in southern and central Europe (Fig. 3).

The impact of climate change on the distribution ranges of these species will depend on their reproductive age and dispersal capacity. In contrast to gymnosperms, angiosperms have more diversified and advanced dispersal strategies (Sádlo et al., 2018). These traits, as well as multiple purposes of introduction, allow them to shorten lag phase of invasion (Kowarik, 1995), which is important limitation of alien tree species dispersal. According to Meier et al. (2012) pioneer species can achieve dispersion rates up to forty times faster than late-successional species. Hence, we can expect that the fast-growing early successional trees *A. negundo*, *A. altissima*, and *F. pennsylvanica* dispersed by wind and water (Drescher and Prots, 2016; Girel et al., 2010; Kowarik and Saumel, 2006; Kowarik and Von Der Lippe, 2006) and *P. serotina* disseminated by birds (Deckers et al., 2008), will spread faster than seeds of *J. nigra* and *Q. rubra* which are produced at older ages and dispersed mainly by rodents, rarely by birds (Bieberich et al., 2016; Dyderski et al., 2020; Nicolescu et al., 2020). However, the jays, being the most common seed-bearing birds, prefer the less bulky seeds of the native oaks (Wróbel et al., 2021). In the case of *Q. rubra*, seed dispersal was observed up to 1.5 km (Riepsas and Straigytė, 2008). Hence the long-distance dispersion of these two heavy-seeded alien species will depend on the deliberate introduction by humans (Nicolescu et al., 2020; Woziwoda et al., 2014).

Pouteau et al. (2021) found that naturalized species may expand their range due to climate change further than those species which are not naturalized. Usually, synanthropic species have broader climatic niches than non-synanthropic, and therefore have higher chances to naturalize in a wider range of climatic conditions. In addition, species from lower elevations can shift ranges further in the latitudinal direction, while species from higher elevations will only shift their ranges higher. Most of the introduced species naturalize at lower altitudes (Medvecká et al., 2018; Pauchard et al., 2009; Pauchard and Alaback, 2004). Hence our predictions indicate that climate niches are shifting mainly in the latitudinal direction (Figs. 2 and 3). Their expansion in northern and northeastern Europe will depend on the rate of decline of native species and the ability to colonize by range-shifting native and alien species, the presence of ecological filters, land development and propagule pressure. Such a case can be similar to the *Pinaceae* invasion in the southern hemisphere, where the competitive pressure from species adapted to local conditions and phylogenetically related species is lower (Peña et al., 2008; Simberloff et al., 2002; Taylor et al., 2016).

The effects of alien gymnosperms in Europe are poorly documented. Most of known evidence comes from studies on *P. menziesii*, whose impact is similar to that of native conifers (Piwczyński et al., 2016; Schmid et al., 2014). *P. strobus*, in contrast, is a transformer tree suppressing regeneration of native trees by enormous litter production and root competition (Hadincová et al., 2007). However, impacts of other species are less recognized. Angiosperms pose a significant threat to Europe's biodiversity. *Q. rubra* negatively affects nutrients cycling, and its leaf litter constitutes a physical barrier to the renewal of other plant species (Chmura, 2013; Dyderski et al., 2020; Stanek et al., 2020). Re-

cent studies have shown the negative impacts of *Q. rubra* on biomass and generative reproduction of *Vaccinium* spp. (Woziwoda et al., 2021), and that the presence of this species may negatively affect food chains in forest ecosystems. On the other hand, species such as *A. altissima*, *A. negundo*, *J. nigra* and *P. serotina*, through allelopathic interactions, can strongly cause alternations in the species composition of plant communities (Bączek and Halarewicz, 2019; Hrib et al., 2017; Straigytė et al., 2015). Possible significant deterioration of growing conditions for the economically most important conifers for Europe (Dyderski et al., 2018; Hanewinkel et al., 2012; Thurm et al., 2018) and possibly increased invasiveness of deciduous species threatening biodiversity in the future suggest that the cultivation of the studied exotic species will result in economic and ecological losses (Castro-Díez et al., 2019; Dyderski and Jagodziński, 2020). Therefore, native species should be considered in the first place for planting in European forests, taking advantage of their geographical variability in adaptation to climatic conditions.

The magnitude of the changes in geographic ranges predicted in this study and in previous studies on other native and non-native tree species in Europe (Dyderski et al., 2018; Puchałka et al., 2021), at a rate never observed before in the Holocene raises concerns that the impacts of ongoing climate change will be dramatic for our planet. There is a risk that local forest ecosystems will be disturbed and that their original ecological function and biodiversity will be significantly affected. Particularly in central, northern and eastern Europe, where forests are dominated by few tree species, it is likely that under changing climate there will be a lack of native trees capable of overcoming this change and creating new vegetation types in balance with the climate. However, this collapse may also be reinforced by forestry practices originally aimed at optimizing this process and maintaining the extent of forest cover. A debatable issue is the impact of introduced non-native tree species, which are intended to replace threatened dominants but may further contribute to the disruption of the damaged ecosystem. The question remains, to what extent the introduction, cultivation and spontaneous spread of alien tree species can help or hinder the establishment of new forest vegetation to maintain the Holocene continuum of forest development?

5. Conclusions

Our study provided a first-time comprehensive overview of predicted shifts in distributions of major alien tree species in Europe under the most recent climate change scenarios, included in the 6th IPCC report. Our models predicted significant losses of climatically suitable areas for all studied conifers except *P. strobus* and a large increase of the climatically suitable areas for the studied deciduous trees. For all species studied, at least half of predicted climatic optimum shifts by 2061–2080 will occur in 2041–2060. Especially for the coniferous species studied, these will be ca. 75% of predicted changes. These predicted shifts are relevant for evidence-based management in sites already occupied by the studied alien tree species and to the development of prevention and early detection measures in areas predicted to become climatically suitable for the studied species.

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Author contributions

RP and MKD: Conceptualization; RP, SPD, JS, MV, SK, YP, MN, VNN, TZ, MM and MKD: data collection; RP, MKD and SPD: data processing, statistical analysis and writing original draft; RP, SPD, AMJ, JS, MV, MK, SK, YP, MN, VNN, TZ and MKD: writing, review and editing. All authors have read and agreed to the final version of the manuscript.

Y materials

Appendix A. Literature data used for filling the gaps of the studied tree species distribution.

Appendix B. Supplementary tables and figures.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Supplementary materials

Supplementary material associated with this article can be found, in the online version, at [doi:10.1016/j.agrformet.2023.109650](https://doi.org/10.1016/j.agrformet.2023.109650).

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